Influence of previous herbivory on behavior and development of *Spodoptera exigua* larvae on glanded and glandless cotton

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Abstract

We examined the influence of previous herbivore injury on the feeding behavior, survival and development of larval beet armyworm, *Spodoptera exigua* Hübner (Lepidoptera: Noctuidae), on glanded and glandless 'Stoneville 213' cotton, *Gossypium hirsutum* L. In a greenhouse study, neonate *S. exigua* placed on the terminal foliage of glanded cotton plants moved down the plant to feed on older leaves. The location of feeding was more concentrated towards the bottom of the plant on previously damaged plants than on undamaged control plants. In contrast, larval feeding on glandless plants was evenly distributed within the plant and no difference in distribution was noted on plants that had sustained previous herbivore injury when compared to undamaged plants. In a laboratory study, where larvae were offered one type of foliage in a no-choice situation, survival on young or mature leaves from glanded or glandless plants, with or without previous herbivore injury, did not differ significantly. However, pupae of larvae reared on young leaves of damaged glanded cotton weighed significantly less than pupae from larvae fed all other diets. Pupae from larvae fed young leaves of control glandless plants weighed significantly more than pupae from all other diets. Similar trends were observed in adult weights. In addition, time to pupation and time to adult emergence were significantly longer for larvae fed young leaves from damaged glanded plants compared to all other diets. The experiments reported here link larval feeding behavior of *S. exigua* to performance. Larval feeding preferences changed following induction of systemic defense such that food choice was optimized for growth.

Introduction

The pioneering study of Green & Ryan (1972) on the induction of proteinase inhibitors in tomato and potato leaves by Colorado potato beetle feeding was the first of many to show that plants respond biochemically to feeding injury by arthropods. Often these induced responses are detrimental to herbivore preference or performance and are thus described as induced resistance (Karban & Baldwin, 1997). Induced resistance may be localized to the tissue where injury occurred or may be systemic, occurring throughout the plant.

Systemic induced resistance in cotton plants, *Gossypium hirsutum* L., has been demonstrated after mite infestation (Karban & Carey, 1984) and lepidopteran larval feeding injury (Alborn et al., 1996). Plants infested at the cotyledonary stage with mites developed true leaves that were less suitable for mite population increase than were uninfested plants. Cotton plants whose oldest true leaves had been damaged by larvae of *Spodoptera exigua* Hübner and *S. littoralis* L. produced new foliage that was less stimulatory to larval feeding compared to that from undamaged plants. Mature leaves from damaged plants, on the other hand, were not deterrent to feeding compared to those leaves from undamaged plants (McAuslane et al., 1997).

Induced resistance to *S. exigua* in newly developed cotton leaves was correlated with increased production of terpenoid aldehydes, such as gossypol and heliocides (McAuslane et al., 1997; McAuslane & Alborn, 1998), and volatile mono- and sesquiterpenes and lipoxygenase products (McAuslane & Alborn, 1998). Cotton leaves which were fully mature at the time of herbivore damage did not contain greater quantities of terpenoid aldehydes than mature leaves of control plants (McAuslane et al., 1997). Glanded cotton, whose leaves contain pigment glands and their associated terpenes (Elzen et al., 1985), mounted a 10-fold stronger systemic response to larval feeding than did glandless cotton, which produced no terpenoid aldehydes, only small quantities of volatile terpenes, but almost three-fold greater quantities of lipoxygenase products (McAuslane & Alborn, 1998).

In our previous studies, feeding preference tests were conducted with *S. exigua* larvae enclosed in an arena with a choice of only two or four food sources (Alborn et al., 1996; McAuslane et al., 1997; McAuslane & Alborn, 1998). In the field, however, *S. exigua* larvae can move within a plant (Akey & Henneberry, 1998) and even between plants to select their food (Smits et al., 1987). In general, young foliage of plants is more nutritious, with higher amounts of water and nutrients, and is less tough than older foliage (Slansky & Scriber, 1985). However, there is a gradient of gland density (McAuslane et al., 1997) and, consequently, terpenoid aldehyde concentrations within the cotton plant from youngest to oldest leaves (H. J. McAuslane & H. T. Alborn, unpubl.). Terpenoid aldehyde concentration in young foliage of previously damaged plants is much higher than that in young leaves from undamaged plants whereas, in mature leaves, terpenoid aldehyde content is similar for damaged and undamaged plants (McAuslane et al., 1997). We hypothesize that, on induced cotton plants, *S. exigua* larvae may alter their feeding behavior to maximize their nutrition and minimize their exposure to deterrent or potentially toxic allelochemicals. If this is the case, growth rate, pupal and adult weights, and/or survival should be maximized by this feeding strategy. Based on the biochemical differences described above (McAuslane & Alborn, 1998), we expect this strategy to differ between glanded and glandless cotton. To test these hypotheses, we studied: 1) the within-plant distribution of feeding damage, and 2) the survival, developmental rate, and pupal and adult weights of *S. exigua* larvae fed young or mature leaves from induced and uninduced glanded and glandless cotton plants.

Materials and methods

Insect and plant material. Beet armyworm eggs were obtained from the USDA-ARS Southern Insects Management Research Unit (Jamie Whitten Delta States Research Center, Stoneville, Mississippi). Larvae used in experiments were either neonates or third instars that had been reared on pinto bean-based artificial diet according to standard practices (King & Leppla, 1984).

'Stoneville 213' glanded cotton and a 'Stoneville 213' glandless isoline were grown in a greenhouse in 12.5-cm diameter pots filled with commercial potting mix (mixture of MetroMix 220 and MetroMix 500, Grace Sierra; Milpitas, CA). The greenhouse was illuminated with natural light and the light cycle ranged from L14:D10 to L12:D12 (60–90% r.h., and 25–40 °C). Plants were watered as necessary and fertilized once at the first-true-leaf stage with approximately 5 g of slow-release-formulation fertilizer (Osmocote 14-14-14, Scotts-Sierra; Marysville, OH).

Infliction of herbivore injury. Herbivore injury was inflicted on glanded and glandless cotton plants when they possessed seven true leaves (approximately 6 weeks old). Two third-instar *S. exigua* larvae were placed on each of the two oldest true leaves of a plant. Each leaf was enclosed in a perforated plastic bag (Ziploc vegetable bags, DowBrands; Indianapolis, IN) sealed with a pipe cleaner twisted gently around the leaf petiole. Control plants received plastic bags and a pipe cleaner but no larvae. Larvae and bags were removed 48 h later.

Feeding behavior of S. exigua. Four isoline × damage treatment combinations were prepared: (1) control (i.e., undamaged) glanded plants, (2) control glandless plants, (3) herbivore-damaged glanded plants, and (4) herbivore-damaged glandless plants. Plants were arranged in a randomized complete block design in the greenhouse with 14 blocks (= replicates). Third-instar larvae inflicting damage on the herbivore-damaged plants had been removed from the plants 2 days previously. Ten neonate *S. exigua* were transferred to a gelatin capsule using a camel's hair brush and then gently tapped out of the capsule onto the second youngest fully expanded leaf of each cotton plant (i.e., seventh leaf from the bottom of the plant).

Larvae were allowed to feed freely within the plant. Surviving larvae were removed from the plants 10 days later and weighed. All leaves, except the

two oldest leaves that received the original feeding injury, were removed from the plants, labeled, placed between acetate sheets, and then photocopied. Small areas of feeding damage were marked with a white pen on the photocopies which were then scanned into a computer. Feeding damage on each leaf was quantified using image analysis software (ImagePC beta version 1, Scion Corporation; Frederick, MD).

Larval recovery was analyzed with a Kruskal-Wallis test (PROC NPAR1WAY, SAS Institute, 1995). Weight of recovered larvae (averaged within replicates) was compared among the four treatment combinations using analysis of variance (PROC GLM, SAS Institute, 1995). Previous experiments had already indicated that larvae would consume more foliage on control plants than damaged plants (Alborn et al., 1996; McAuslane et al., 1997; McAuslane & Alborn, 1998). Therefore, our goal in this study was to compare the location of feeding within the plant, not the absolute amounts of feeding. Thus, amount of each leaf consumed was converted to a proportion of the total consumption on each plant. The distribution of consumption within a plant was compared between control and damaged plants on each isoline separately using a log-likelihood ratio goodness of fit test (Zar, 1984). By the end of the experiment, plants had developed axillary leaves at nodes one to eight, in addition to the approximately 10 main stem leaves. Consumption of axillary leaves on a plant was expressed as a proportion of the total consumption on that plant. The proportion consumed on axillary leaves was compared between control and damaged plants for each isoline separately using a Wilcoxon two-sample test (PROC NPAR1WAY, SAS Institute, 1995).

Survival and development of S. exigua. Four isoline × damage treatment combinations were set up as in the previous experiment. Larvae inflicting herbivory on the damaged plants were removed from the plants 6 days before foliage was excised for use in the experiment.

The experiment was set up in a climate-controlled room with environmental conditions of L14:D10, 28 °C day/25 °C night, and 30–45% r.h. Light was provided over the bench by four 110-W cool-white fluorescent lights. Three third-instar larvae were weighed together and placed in a clear plastic box with a lid (7.5 × 7.5 × 7.5 cm). We then added either the terminal shoot of a cotton plant (= 'young'), containing the three youngest leaves that had expanded to at least 3 cm in diameter or three older leaves (= 'mature')

that were true leaves three, four, and five from the bottom of the plant. The petiole of the terminal or the three petioles of the mature leaves were placed in a 1.5-ml plastic eppendorf vial with a water-moistened cotton ball. Foliage in all boxes was replaced 4 days later and again 1 day later if larvae had consumed more than 75% of the foliage. Leaves were not limiting to larval feeding at any time and they remained turgid throughout the experiment. We examined the boxes once per day and recorded time to pupation, pupal weight, time to adult emergence, adult weight, and survival from third instar to adult emergence. Eight blocks (= replicates) of the eight treatment combinations (damage × isoline × leaf age) were arranged in a randomized complete block design and were placed on a laboratory bench.

Pupal and adult weights and days to pupation and adult emergence were analyzed as a three-factor factorial experiment using analysis of variance (PROC GLM, SAS Institute, 1995). Initial larval weight was included as a covariate in the analysis of pupal and adult weight. Least squares means were separated using the probability of a significant difference ($\alpha = 0.05$). Survival was compared among the four damage × leaf age combinations separately for glanded and glandless isolines using a Kruskal–Wallis test (PROC NPAR1WAY, SAS Institute, 1995).

Results

Feeding behavior of S. exigua. Of the 10 larvae originally placed on each plant, we only recovered from zero to six larvae, now in the third instar, 10 days later. We recovered the most larvae from the control glandless plants and the fewest from the damaged glanded plants (Table 1); however, larval recovery did not differ significantly among the four plant types. Larvae that were not recovered may have suffered mortality by attempting to disperse from an unsatisfactory food source by dropping down from a silk thread and falling to the ground below the greenhouse benches. In addition, larvae may have been preyed upon by ants or lizards observed in the greenhouse. However, predation was unlikely to be a significant source of mortality for larvae still on plants because, when we noticed a few ants on the plants the day after we released neonate larvae, we removed all ants and applied a Tanglefoot barrier to plant stems to prevent recolonization. Lizards were too heavy to forage on the plants but may have eaten larvae that fell to the greenhouse bench.

Table 1. Number and average weight of *S. exigua* larvae recovered from plants after feeding for 10 days on glanded or glandless 'Stoneville 213' cotton with or without previous feeding damage

Isoline × damage combination		No. of replicates	Total no. of larvae recovered[a]	Avg. larval weight, mg (mean ± s.d.)[b]
Glanded				
	Control	14	25	11.6 ± 5.2 b
	Damaged	14	19	12.2 ± 5.6 b
Glandless				
	Control	14	32	30.2 ± 14.6 a
	Damaged	14	28	17.5 ± 6.3 b

[a]Totals did not differ significantly (χ^2, $P > 0.05$).
[b]Means followed by a different letter differed significantly (probability of a significant difference of least squares means, $\alpha = 0.05$).

The weight of larvae recovered from the four isoline × damage combinations differed significantly, with larvae recovered from the control glandless plants weighing more than those from the other three plant types (Table 1). The effects of isoline (F = 21.60; df = 1, 32; P = 0.0001) and damage (F = 7.97; df = 1, 32; P = 0.0081) were significant, as was their interaction (F = 10.43; df = 1, 32; P = 0.0029).

The distribution of consumption within glanded cotton differed significantly between control and damaged plants (log-likelihood, G = 70.25; df = 9; P < 0.001). Larvae consumed very little of the youngest or oldest main stem leaves on control glanded plants; most of the feeding occurred in the middle portion of the plant (Figure 1A). However, larval consumption on previously damaged glanded plants was shifted downwards on the plant compared to that on control plants (Figure 1A). This difference in distribution of larval feeding can be seen more clearly in Figure 2A where consumption is categorized according to its position relative to the leaf on which larvae were originally released: (1) the leaf on which larvae were released ('on' – usually leaf seven), (2) the leaves above the site of initial larval placement ('above'), or (3) the leaves below the site of initial placement ('below'). The distribution of damage within control and damaged plants differed significantly (G = 23.85; df = 2: P < 0.001) with less consumption above or at the site of release of larvae and more consumption below the site of original infestation on damaged plants than on control plants. Finally, the location of feeding injury, either on the main stem leaves or the axillary leaves, differed significantly between damaged and control glanded plants (Wilcoxon two-sample test, S
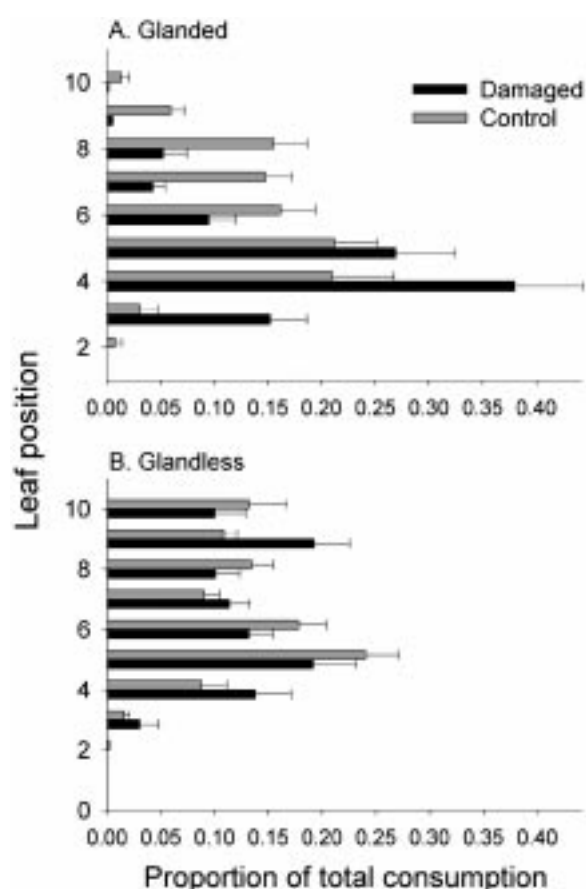

Figure 1. Location of main-stem leaf consumption by *S. exigua* larvae allowed free movement within (a) glanded and (b) glandless 'Stoneville 213' cotton plants in a greenhouse experiment. Leaf two is the oldest and leaf 10 is the youngest leaf on a plant. Bars indicate one standard error of the mean.

Table 2. Average percent survival of cohorts of three *S. exigua* larvae fed excised foliage of 'Stoneville 213' cotton in a laboratory experiment

Isoline × damage × leaf age combination	No. of replicates	Mean ± s.d.[a]	
		Survival to pupal stage	Survival to adult stage
Glanded control			
'Mature'	8	92 ± 14	88 ± 16
'Young'	8	92 ± 14	86 ± 16
Glanded damaged			
'Mature'	8	83 ± 24	75 ± 22
'Young'	8	88 ± 23	75 ± 36
Glandless control			
'Mature'	8	88 ± 16	67 ± 17
'Young'	8	92 ± 14	79 ± 23
Glandless damaged			
'Mature'	8	96 ± 11	83 ± 24
'Young'	8	79 ± 23	62 ± 20

[a]Means within a cotton isoline did not differ significantly (Kruskal–Wallis test, P >0.05).

= 264.0; P = 0.0049). Of the total feeding on control plants, 3.4% occurred on the axillary leaves (which developed during the course of the experiment and are therefore 'young') whereas only 0.9% occurred on axillary leaves of damaged plants.

Consumption within glandless plants appeared relatively uniform except for reduced consumption on the oldest leaf, leaf three (Figure 1B). There was no significant difference in feeding pattern between control and damaged plants (G = 14.73; df = 9; 0.05 < P < 0.1). Consumption above and below the site of original larval release was very similar and did not differ significantly between control and damaged plants (G = 1.62; df = 2; P > 0.75, Figure 2B). In addition, the location of feeding injury, either on the main stem leaves or the axillary leaves, did not differ significantly between damaged and control glandless plants (Wilcoxon two-sample test; P > 0.05) with 8.6% of total feeding on control plants occurring on axillary leaves and 9.6% occurring on axillary leaves of damaged plants.

Survival and development of S. exigua. Survival to the pupal or adult stage did not differ significantly on the four damage × leaf age combinations on either cotton isoline (Kruskal-Wallis test; P > 0.05) (Table 2). However, there were significant differences in pupal weights on the eight diets (Table 3). All interaction terms were significant sources of variability for pupal weights as were the individual factors of isoline, damage, and leaf age. The pupae of larvae fed young
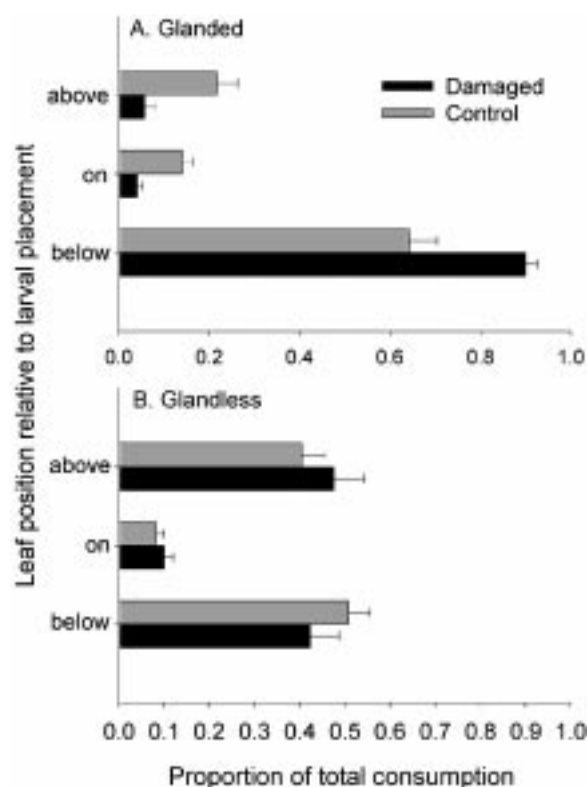

Figure 2. Location of main-stem leaf consumption by *S. exigua* larvae on (a) glanded and (b) glandless 'Stoneville 213' cotton according to leaf position relative to site of original larval release: 'on' – consumption on leaf seven where neonate larvae were released; 'above' – consumption on leaves above site of larval release; 'below' – consumption on leaves below site of larval release. Bars indicate one standard error of the mean.

Table 3. ANOVA table for influence of isoline, plant damage, and leaf age on pupal and adult weights of *S. exigua* fed excised 'Stoneville 213' cotton foliage from third-instar stage until pupation in a laboratory experiment

Factor	df	F	P
Pupal weight			
Isoline	1,48	55.72	0.0001
Damage	1,48	40.32	0.0001
Leaf age	1,48	11.55	0.0014
Replicate	7,48	1.91	0.0893
Initial larval weight[a]	1,48	18.86	0.0001
Isoline × damage	1,48	14.18	0.0005
Isoline × leaf age	1,48	29.82	0.0001
Damage × leaf age	1,48	38.25	0.0001
Isoline × damage × leaf age	1,48	5.27	0.0261
Adult weight			
Isoline	1,48	16.50	0.0002
Damage	1,48	12.86	0.0008
Leaf age	1,48	2.43	0.1257
Replicate	7,48	1.04	0.4173
Isoline × damage	1,48	2.12	0.1516
Isoline × leaf age	1,48	5.92	0.0188
Damage × leaf age	1,48	13.09	0.0007
Isoline × damage × leaf age	1,48	7.67	0.0080

[a]Initial larval weight was included as a covariate in the model when it was a significant source of variation.

foliage from the glandless control plants weighed 5.3–33.7% more than pupae in the other treatments, while pupae of larvae fed young foliage from damaged glanded plants weighed 16.7–25.2% less than those in all other treatments (Table 4). It appears that mature and young leaves of control glanded plants were similarly suitable for larval growth. However, damage to glanded plants caused the young leaves to become much less suitable for growth than mature leaves. In glandless plants, the diet of young leaves of control plants produced pupae that weighed 6.0% more than pupae reared on the diet of mature leaves. Damage to glandless plants caused the young leaves to become less suitable and pupal weights of larvae fed mature and young leaves were similar.

Adult weight was influenced by the main effects of isoline and damage and the interactions of damage × leaf age, isoline × leaf age, and isoline × damage × leaf (Table 3). In glanded plants, diets of young or mature leaves from control plants and mature leaves from damaged plants, produced adults of similar size. However, larvae fed young leaves from damaged plants produced adults weighing 28.8–33.8% less than those on other glanded treatments (Table 4). In glandless plants, damage or leaf age did not influence adult weights and all diets produced larger adults than those produced on young leaves from damaged glanded plants.

Time to pupation was influenced by the main effects of isoline (F = 17.48, df = 1, 48, P = 0.0001), damage (F = 13.86, df = 1, 48, P = 0.0005), and leaf age (F = 22.60, df = 1, 48, P = 0.0001), and the interaction of isoline × leaf age (F = 8.53, df = 1, 48, P = 0.0053). In both control and damaged glanded plants, larvae took 0.5 and 1 day longer, respectively, to pupate when fed young leaves than when fed mature leaves (Table 4). Larvae fed young leaves of damaged glanded plants took 0.6–1.1 days longer to pupate than larvae fed other diets of glanded cotton. In glandless plants, larvae pupated at the same time when fed mature or young leaves from control plants. Pupation was also similar between young and mature leaves on damaged glandless plants but pupation was delayed 0.4 days for larvae fed on young leaves from damaged plants compared to leaves from control plants.

Time to adult emergence was influenced by the main effects of isoline (F = 16.11, df = 1, 48, P = 0.0002), damage (F = 12.73, df = 1, 48, P = 0.0008), and leaf age (F = 7.86, df = 1, 48, P = 0.0073), and the interaction of damage × leaf age (F = 8.22, df = 1, 48, P = 0.0061). In glanded plants, time to adult emergence was 1.2–1.4 days longer for larvae fed on young leaves from damaged plants than for larvae fed all other types of glanded foliage (Table 4). In glandless plants, adults emerged more quickly after feeding on leaves of control plants than on young leaves of damaged plants. Time to emergence was 0.7–0.9 days longer on control glanded plants than on control glandless plants.

Discussion

Like most other lepidopteran larvae, the immature stages of *S. exigua* are quite mobile. The larvae can readily move within a plant (Smits et al., 1987; Ruberson et al., 1994), moving from the lower portion of the plant where the female oviposits, up the plant as the larvae mature. Larvae can also move between plants (Smits et al., 1987). In this way, they can, to some extent, choose what they will eat. When we placed neonate *S. exigua* on the second youngest leaf of glanded and glandless cotton plants that had been

Table 4. Average pupal and adult weights and days to pupation and adult emergence of *S. exigua* larvae fed excised foliage of 'Stoneville 213' cotton in a laboratory experiment

Isoline × damage × leaf age combination	Mean ± s.d.[a]			
	Pupal weight (mg)	Adult weight (mg)	Days to pupation	Days to adult emergence
Glanded control				
'Mature'	93.8 ± 3.9 bc	51.4 ± 4.8 b	5.5 ± 0.4 cd	14.2 ± 0.4 b
'Young'	94.6 ± 5.0 bc	55.3 ± 2.9 ab	6.0 ± 0.3 b	14.3 ± 0.6 b
Glanded damaged				
'Mature'	89.4 ± 6.1 c	53.6 ± 7.0 ab	5.6 ± 0.3 bcd	14.0 ± 0.3 bc
'Young'	74.5 ± 6.7 d	36.6 ± 7.0 c	6.6 ± 0.4 a	15.4 ± 0.9 a
Glandless control				
'Mature'	93.7 ± 4.5 bc	56.2 ± 5.9 ab	5.4 ± 0.2 d	13.5 ± 0.8 c
'Young'	99.6 ± 5.7 a	59.0 ± 9.2 a	5.4 ± 0.4 d	13.4 ± 0.7 c
Glandless damaged				
'Mature'	94.0 ± 3.4 b	54.1 ± 4.5 ab	5.6 ± 0.5 cd	13.9 ± 0.8 bc
'Young'	91.6 ± 3.8 bc	54.1 ± 8.4 ab	5.8 ± 0.4 bc	14.4 ± 0.7 b

[a] Means within a column followed by the same letter did not differ significantly (probability of a significant difference of least squares means, $\alpha = 0.05$).

previously damaged or not and watched larval movement in the greenhouse, we observed young larvae hanging from silk threads, attempting to disperse. In the field, where plants are densely planted, larvae can move between host plants using this behavior. In our experiment in the greenhouse, leaves of adjacent plants did not touch each other and larvae that spun down on a thread likely fell through the wire-mesh bench to the ground below and could not colonize another plant. Therefore, we hypothesize that the high mortality of larvae that we observed in our greenhouse experiment (77–86%) was due to the fact that larvae were not allowed to exert much choice of where to feed. Those larvae that attempted to locate another plant, as they may do in nature when faced with an unpalatable food source, died in their endeavor. Our data on the distribution of feeding injury was therefore generated by only those larvae that chose to remain on their original host plant.

It has been shown for another cotton pest, *Helicoverpa zea* (Boddie), that more neonates dropped off glanded 'Stoneville 213' (8%) than off the glandless isoline (2%); however, larval behaviors on the plant, such as locomotion and resting, did not differ significantly (Schmidt et al., 1988). In our experiments, larval recovery after 10 days on the plants did not differ significantly (Table 1); however, the position within the plant of the remaining larvae did differ significantly on the four plant treatments. Larvae on control glanded plants moved down from their point

of release to feed on older leaves. However, larval feeding below the site of release on damaged glanded plants was even greater than on control plants. We suggest that it is the high concentration of terpenoid aldehydes in young foliage, and especially young foliage from damaged plants (McAuslane et al., 1997), that caused this behavior. In fact, there is a gradient of increasing levels of terpenoid aldehydes from the oldest to the youngest leaves of both damaged and control glanded cotton plants (H. J. McAuslane & H. T. Alborn, unpubl.) that is positively correlated with the gradient of pigment gland density within plants (McAuslane et al., 1997). In contrast, feeding location in glandless plants was not influenced by previous injury and about 50% of feeding occurred above the site of release in both control and damaged plants. These plants lack terpenoid aldehydes in detectable levels (McAuslane & Alborn, 1998) and larvae are able to feed on the youngest tissue without encountering feeding deterrents. Observation of reduced feeding on the axillary leaves of damaged compared to control glanded cotton is consistent with the avoidance of feeding deterrents, probably terpenoids or volatile terpenes. Probably as a consequence of lack of feeding deterrents, the weight of surviving larvae was higher on control glandless plants than on any other plant type (Table 1).

Our laboratory study indicated that there were significant negative consequences for the fitness of larvae if they were forced to feed on young foliage of dam-

aged glanded plants. Weights of pupae and adults were significantly lower and development times to pupal or adult stages were significantly longer compared to those of larvae fed on mature leaves from damaged glanded plants. Thus, the behavior of dispersing to feed lower down on damaged glanded plants was advantageous. On control glanded plants, weights and development time were similar on young and mature leaves. So, there was no advantage to avoiding the greater quantities of allelochemicals in young leaves by feeding on older leaves which were presumably nutritionally less adequate.

In glandless plants, the youngest leaves of control plants were the most suitable for larval growth because pupal weights on this diet were higher than on mature leaves or leaves from damaged glandless plants. The advantage to feeding on young leaves was not statistically significant for the other three life history parameters measured. Glandless plants do not contain terpenoid aldehydes (McAuslane & Alborn, 1998) and are subject to heavy attack by many generalist herbivores (Bottger et al., 1964; Jenkins et al., 1966). However, damage to glandless plants renders young leaves less suitable for development than their undamaged counterparts making them more like mature leaves in suitability for larval growth. Thus, some damage-induced changes must have occurred, but these remain to be identified.

Spodoptera littoralis neonates that were fed excised foliage of glanded 'DPL 90' cotton developed equally well on induced and control plants (Anderson & Alborn, 1999). In this study, the larvae were provided both young and mature leaves from the plants and could, therefore, have chosen to feed on older leaves that, presumably, did not have elevated levels of terpenoid aldehydes. In addition, or alternatively, these two *Spodoptera* species may differ in their physiological and behavioral responses to cotton allelochemicals. In support of this last statement, Agrawal & Karban (2000) reported that *S. exigua* larvae placed on cotton plants as neonates and allowed to feed for 8 days were significantly smaller on glanded than on glandless plants. In addition, feeding on systemically induced plants that had been damaged by mite feeding and had elevated numbers of pigment glands reduced larval growth even further, with induced resistance in glanded plants being three times as strong as induction in glandless plants.

In many studies of lepidopteran feeding on glanded and glandless cotton, larval fitness is reduced when larvae are reared on glanded plants in no-choice situations. For example, *Earias vittella* (F.) had reduced larval survival, pupation, larval and pupal weights, and increased time to pupation when reared on leaves from glanded cotton than on leaves of glandless cotton (Dongre & Rahalkar, 1980). *Heliothis virescens* (F.) fed a diet of cotton cotyledons had reduced survival, reduced rate of development, and reduced larval and adult weights on glanded cotton compared to glandless cotton (Montandon et al., 1986). However, these negative effects on *H. virescens* growth rate were not due to reduced consumption rate of glanded cotton but rather a decrease in efficiency of conversion of ingested food to body substance (Montandon et al., 1987). Even though *H. zea* larvae grew more slowly on gossypol-laced diets compared to control diets, consumption rate was not significantly reduced (Oliver et al., 1970). *Heliothis virescens* relative growth but not relative consumption was reduced on glanded cotton compared to glandless cotton (Mulrooney et al., 1985).

In contrast to the studies with *H. virescens* and *H. zea*, we suspect that *S. exigua* is avoiding consumption of leaves with high levels of allelochemicals. This is suggested by movement within the plant away from leaves with high levels of allelochemicals and results from our previous choice studies (Alborn et al., 1996; McAuslane et al., 1997; McAuslane & Alborn, 1998). In no-choice situations, larvae probably have reduced consumption associated with allelochemical deterrency. However, we cannot determine whether there is an antibiotic effect of allelochemicals in foliage from induced plants, in addition to the antixenotic effect, without more closely quantifying feeding and determining nutritional indices. We can conclude from this study however, that feeding behavior of larval *S. exigua* was changed drastically on previously damaged glanded plants and very much less so on previously damaged glandless plants. The change in feeding behavior increased larval fitness and was likely allelochemically mediated. Although we only examined one pair of glanded and glandless cotton isolines in this study, it is likely that we would obtain similar results with other pairs, if indeed, as we believe we have shown previously (McAuslane et al., 1997; McAuslane & Alborn, 1998), feeding deterrence to *S. exigua* is caused by the presence of pigment glands and their associated terpenoid aldehydes.

Acknowledgements

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